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Macroscale patterns of synchrony identify complex relationships among spatial and temporal ecosystem drivers

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Abstract. Ecology has a rich history of studying ecosystem dynamics across time and space that has been motivated by both practical management needs and the need to develop basic ideas about pattern and process in nature. In situations in which both spatial and temporal observations are available, similarities in temporal behavior among sites (i.e., synchrony) provide a means of understanding underlying processes that create patterns over space and time. We used pattern analysis algorithms and data spanning 22–25 yr from 601 lakes to ask three questions: What are the temporal patterns of lake water clarity at sub-continental scales? What are the spatial patterns (i.e., geography) of synchrony for lake water clarity? And, what are the drivers of spatial and temporal patterns in lake water clarity? We found that the synchrony of water clarity among lakes is not spatially structured at sub-continental scales. Our results also provide strong evidence that the drivers related to spatial patterns in water clarity are not related to the temporal patterns of water clarity. This analysis of long-term patterns of water clarity and possible drivers contributes to understanding of broad-scale spatial patterns in the geography of synchrony and complex relationships between spatial and temporal patterns across ecosystems.

Key words: lake; long-term; Secchi; space-for-time substitution; synchrony; water clarity.

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Introduction

Ecology has a rich history of studying ecosystem dynamics across time and space that has been motivated by both practical management needs and the need to develop basic ideas about pattern and process in nature (Wiens 1989, Turner et al. 2001). To study spatial patterns, ecologists have typically used single point in time samples from multiple systems distributed across a variety of spatial gradients, whereas temporal patterns are typically revealed through an examination of one or a few well-sampled systems. Indeed, spatially extensive data are often used to compensate for the deficit in long-term data via studies using space-for-time substitutions (Pickett 1989, Fukami and Wardle 2005, Lester et al. 2014). Ecologists have long recognized that this approach is an imperfect substitute for long-term studies because it assumes that processes that create differences among sites also determine change through time —an assumption that may not always be met (Pickett 1989, Fukami and Wardle 2005). In situations in which both spatial and temporal observations are available, similarities in temporal behavior among sites (i.e., synchrony) provide a means of understanding underlying processes that create patterns over space and time (Magnuson et al. 2004). If the space-for-time assumption holds, then sites in a landscape that are similar may also be expected to be synchronous. Further, synchronous behavior among a pair of ecosystems suggests shared drivers and responses to those drivers. Thus, examination of spatial aspects of synchrony should reveal the processes shaping these patterns (the geography of spatial synchrony, sensu Walter et al. 2017), providing a means of evaluating how or if space-for-time approaches may be used.

Lakes represent a useful model system for studying spatial and temporal patterns. Across large areas, variation among lakes across space (e.g., lake water quality; Read et al. 2015) and through time (e.g., ice cover, temperature, hypoxia, and salinity; Magnuson et al. 2000, O'Reilly et al. 2015, Jenny et al. 2016, Dugan et al. 2017) can often be explained by a combination of drivers acting at multiple spatial scales (i.e., ecological context). There is also a long history of studying synchrony in lakes, albeit mainly at local to regional spatial extents (e.g., Magnuson et al. 1990, Soranno et al. 1999, Jane et al. 2017). The presence of both local- and regional-scale drivers provides a compelling challenge for considering spatial patterns in synchrony and the capacity to infer processes shaping both spatial patterns and temporal dynamics.

Although data scarcity has been a constraint for understanding long-term change, datasets are becoming longer, and integrated databases covering broad spatial extents are emerging (O'Reilly et al. 2015, Read et al. 2017, Soranno et al. 2017). Extensive datasets of lake water clarity are notable (e.g., Lottig et al. 2014) because this ecosystem variable has been measured consistently for many decades and across many regions and countries using simple, reliable equipment (i.e., a Secchi disk). Water clarity plays an important role in regulating many physical, chemical, and biological dynamics within lakes and is responsive to changing ecological context such as land use conversion (Bruhn and Soranno 2005), climate change (Gunn et al. 2001, Rose et al. 2017), and introduction of invasive species (Walsh et al. 2016). However, few studies have examined how water clarity in a large number of lakes in different settings has changed through time.

We used pattern analysis algorithms and data spanning 22–25 yr from 601 lakes across 1,800,000 km^2 to ask three questions: What are the temporal patterns of lake water clarity at sub-continental scales? What is the geography of spatial synchrony for lake water clarity? And, what are the drivers of spatial and temporal patterns in lake water clarity? Depending on the answers to these questions, there are three possible outcomes that will help infer the likely underlying processes controlling the spatial and temporal patterns in water clarity: (1) If regional ecological context (e.g., climate) drives lake water clarity over time, then lakes within regions should be synchronous and temporal patterns should be associated with climate (or other regional-scale) variables (2) if local ecological context (e.g., watershed area, lake depth) drives water clarity over time, then lakes that are synchronous may be dispersed across regions but share similar local features; or (3) if ecological context at multiple different scales (e.g., regional climate and local watershed characteristics) interact (i.e., cross-scale interactions; Peters et al. 2007) to influence water clarity over time, then there should be complex spatial and temporal patterns such that synchrony among lakes is not spatially structured, nor strongly related to local features.

Methods

We used lake water clarity observations, measured as Secchi depth readings (hereafter water clarity) from the Lake GeoSpatial temporal database (LAGOS-NE_{LIMNO} version 1.054.01; Soranno et al. 2015, Lottig et al. 2017) from the northeastern-most 17 U.S. states (Fig. 1). We restricted our analysis to measurements taken between 15th June and 15th September when most lakes in the study

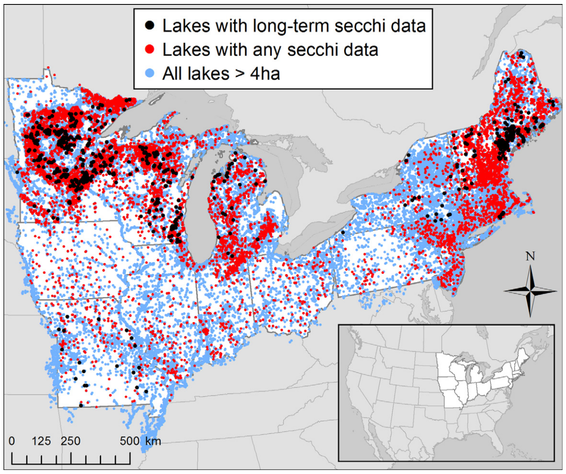

Fig. 1. Spatial extent of LAGOS-NE database and this study including all lakes greater than four hectares (blue), all lakes that have at least a single water clarity measurement (11,348 lakes; red), and the 601 lakes included in this study with 22 + yr of water clarity data (black).

area are thermally stratified and to lakes with at least a single summer value for 22 + yr between 1987 and 2012. For each lake and year, we calculated the median summer water clarity value. The final dataset contained 601 lakes with 22–25 (median = 24) annual estimates of water clarity for each individual lake (Fig. 2). Of the 14,212 annual estimates of water clarity generated in this study, only 2% were based on a single observation and the median number of discrete water clarity measurements for each of the 601 lakes over the 25-yr study period was 223 with a median intra-annual coefficient of variation of approximately 16%. Water clarity time series were standardized ($u = 0$, $\sigma = 1$) to account for differences in scale.

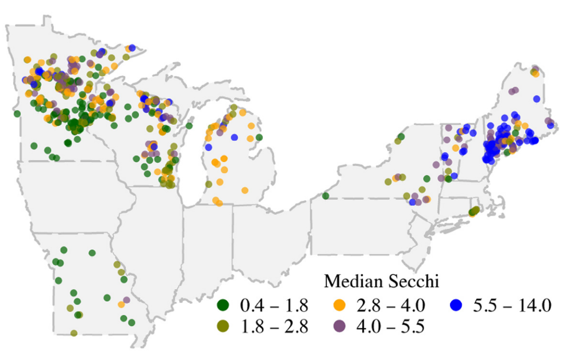

Fig. 2. Median water clarity values from the 22 + yr records for each of the 601 lakes included in this study.

We also examined several variables that describe the ecological context (hereafter drivers) of each individual lake (Table 1) from LAGOS-NE$_{GEO}$ (version 1.03; Soranno et al. 2015, 2017), including lake characteristics such as surface area and maximum depth, climate variables including annual and 30-yr normal of precipitation and temperature (Arguez et al. 2012), and landscape characteristics such as watershed area, land use/land cover, and annual average runoff (Gebert et al. 1987). Detailed information about the variables used in this study (Table 1) is found in the Supplemental Files of Soranno et al. (2015). In addition to the drivers listed in Table 1, annually resolved (i.e., 25-yr record) values for mean temperature and total precipitation were derived from monthly PRISM data at the HUC8 spatial scale.

We clustered lakes that shared similar long-term water clarity patterns using kernel k-means clustering (Schölkopf et al. 1998) to identify groups of synchronous lakes (sensu Finazzi et al. 2015). We employ dynamic time warping (DTW; Berndt and Clifford 1994) as the distance measure for our kernel k-means because it allowed us to measure time series that contained missing values and account for small time lags between the time series. First, DTW aligns two time series to account for any lags before computing their pairwise distance. We allowed time series to lag ± 1 yr. The DTW distance for a pair of lakes is then computed based on the minimum distance of all possible alignments of their water clarity time series. Kernel k-means clustering with DTW distance measure was implemented in Matlab (R2015). We use the Gaussian radial basis function to transform the DTW distances to their kernel similarities and assign each lake to the cluster with highest average kernel similarity.

We relied on a combination of two factors to discern the number of long-term water clarity patterns. First, we examined scree plots for a sharp break that indicates increases in similarity within each cluster (Jain and Dubes 1988, Appendix S1: Fig. S1a). However, no sharp break existed; a gradual transition occurred between 8 and 15 clusters such that the increase in similarity between lakes within each cluster (measured as a decrease in DTW distance) approximated the decrease that would have occurred from increasing the number of clusters randomly. We used silhouette coefficients to determine the most

Table 1. Ecological context variables used to explain the spatial and temporal patterns in water clarity

Ecologic context characteristics	Variables	Spatial extent of calculation
Lake and watershed characteristics	Lake area (ha)	Lake
	Maximum lake depth (m)	Lake
	Median Secchi depth of lake across time (m)	Lake
	Lake connectivity class (categorical)†	Lake
	Watershed area (ha)	Watershed
	Watershed area/lake area ratio (unitless)	Watershed
	Slope of land around each lake‡ (degrees)	100-m, 500-m buffer, and watershed
	Terrain roughness index§ (m)	100-m, 500-m buffer, and watershed
Watershed land use/cover	Open water (%)	100-m, 500-m buffer, and watershed
	Developed, open space (%)	100-m, 500-m buffer, and watershed
	Developed, low intensity (%)	100-m, 500-m buffer, and watershed
	Developed, medium intensity (%)	100-m, 500-m buffer, and watershed
	Developed, high intensity (%)	100-m, 500-m buffer, and watershed
	Barren land (%)	100-m, 500-m buffer, and watershed
	Deciduous forest (%)	100-m, 500-m buffer, and watershed
	Evergreen forest (%)	100-m, 500-m buffer, and watershed
	Mixed forest (%)	100-m, 500-m buffer, and watershed
	Shrub/scrub (%)	100-m, 500-m buffer, and watershed
	Grassland (%)	100-m, 500-m buffer, and watershed
	Pasture/hay (%)	100-m, 500-m buffer, and watershed
	Cultivated crops (%)	100-m, 500-m buffer, and watershed
	Woody wetlands (%)	100-m, 500-m buffer, and watershed
	Emergent herbaceous wetlands (%)	100-m, 500-m buffer, and watershed
Climate	30-yr normal precipitation (mm)	HUC 12
	30-yr normal temperature (degrees C)	HUC 12
	Categorical value grouping annual temperature patterns	HUC 8
	Categorical value grouping annual precipitation patterns	HUC 8
Hydrology	Runoff (in/year)	HUC 12
	Baseflow index (%)	HUC 12

† Isolated (lakes with no inflow or outflow permanent streams), headwater (lakes at the headwater of a stream network), drainage (lakes connected to surface waters through inflow streams, with no upstream lakes ≥10 ha), drainage-UPLK (lakes connected to surface water through inflowing streams, with at least one upstream lake ≥10 ha).

‡ Mean of the slope of the cells within the zone, where the slope is calculated as the slope at each cell with respect to its immediate neighbors (the cell size is 10 m square).

§ Mean terrain ruggedness index (TRI) of cells within the zone, where TRI at each cell is the absolute difference in meters between the elevation of the focal cell and its immediate neighbors (the cell size is 10 m square).

appropriate number of clusters within this range (8–15 clusters). These coefficients, which range from −1 (less similar) to 1 (more similar), identify how similar a specific water clarity time series is to its assigned cluster along with how it compares to other clusters (Rousseeuw 1987). Mean silhouette coefficient for each set of clusters and the percentage of clusters that had positive mean silhouette coefficients (Appendix S1: Fig. S1a) suggested that the long-term water clarity patterns were best characterized by eight groups of synchronous lakes (i.e., clusters).

Once clusters were identified, we fitted models to quantify the average temporal trend across all lakes in each cluster. A normal distribution was assumed for standardized water clarity at site i and year $t(y_{t,i})$, and the model was as follows.

$$y_{i,t} = N(\alpha + \eta_i + y_t, \sigma^2)$$

where α is the overall intercept, η_i is a random lake effect (an adjustment to the overall intercept, allowing each lake to differ in average water clarity; $\eta_i \sim N(0, \sigma_\eta^2)$), and y_t is a random year effect, representing the common temporal trend for all lakes in a given cluster. Bayesian estimation was used for parameter estimates, where diffuse priors were used for α and σ_η, and a Gaussian random walk prior of order 1 was used for the temporal random effect (Wagner et al. 2016). All models were fitted in WinBUGS executed from within R (R Core Team 2017). To assess convergence, we examined the scale reduction factor for each parameter as well as examined trace plots. All results are summarized as posterior means and 95% credible intervals.

To identify the spatial drivers of water clarity, we fit the lake-specific median water clarity value to driver variables that characterize the ecological setting of lakes (see Table 1) using random forest (RF) models in regression mode (Liaw and Wiener 2002; 10,001 trees). To interpret which individual drivers were related to median water clarity, the most important predictor variables were identified using RF variable selection (Genuer et al. 2015). To further determine the ecological relevance of predictor variables, we derived an estimate of effect size (Read et al. 2015) that characterized the average magnitude of functional responses to specific predictor variables. Finally, to identify the drivers of long-term water clarity patterns, we used RF models, as described above, except in classification mode to quantify the relationships between driver variables (Table 1) and groups of synchronous lakes (i.e., cluster membership). Because the number of lakes was not balanced across the eight cluster categories (median = 72, min = 44, max = 138), the sample size drawn from each category was set to the minimum number of lakes in each group. In essence, this analysis determines whether lakes that share common long-term water clarity patterns also share similar ecological setting attributes.

The ecological setting variables that we included in the above RF model were static and thus are not temporally resolved. We used autoregressive moving average with exogenous inputs (ARMAX) models (Hyndman and Khandakar 2008) to examine whether long-term patterns in climate were related to long-term patterns in water clarity (sensu Rose et al. 2017). Autoregressive moving average with exogenous inputs models are similar to standard ARMA models, which can represent a wide variety of ecological processes (Ives et al. 2010), except they include temporal independent variables (X). These models were fit with annually resolved total precipitation and mean summer temperature as the independent variables. Model results were summarized using the total variance explained by the ARMAX models.

All statistics, unless otherwise described, were conducted using R (R Core Team 2017). All water clarity, geophysical, and climate data are available online (Lottig et al. 2017).

Results

We identified eight synchronous patterns across the study region (Fig. 3). Qualitatively, the patterns can be classified as linear increases (Cluster 2), cycles of differing frequencies (Clusters 1, 3, 5, 6), thresholds (Clusters 7 and 8), and relatively stationary (i.e., minimal change; Cluster 4). The spatial distribution of lakes from which these patterns emerged was not constrained to any specific area within the study region (Fig. 4). All eight clusters were distributed across the entire latitudinal and longitudinal gradients contained in the study extent. In other words, there was little evidence of spatially structured synchrony in water clarity at macroscales. However, the patterns observed in Cluster 6 were most common in the northeastern region and those in Cluster 4 were most common in the southwestern-most region of the study extent.

Multiple lines of evidence suggest that distance between lakes had little influence on strength of synchrony among lakes. The normalized frequency of lakes separated by the equal spatial distances belonging to the same cluster (i.e., synchronous long-term pattern) vs. a different cluster (i.e., asynchronous long-term pattern) was virtually identical across the entire sub-continental spatial extent (Fig. 5a). Likewise, an analysis of synchrony between all lake pairs (Fig. 5b) indicated that sometimes the most synchronous lake (measured using Pearson's correlation coefficient) was located nearby and other times the most synchronous lake was located 2000+ km away. Approximately 9% of the most synchronous lake pairs were located within 50 km, while the remaining 91% were relatively equally distributed across the remaining sub-continental spatial extent captured in this study (Fig. 5c).

We found that 12 measures of ecological context explained 70.7% of the variation in median water clarity in our 601 lakes (Appendix S1: Fig. S2). The top five predictors explained 63.3% of the variation—maximum lake depth, drainage basin-to-lake area ratio, percent woody wetlands within the 500-m buffer around a lake, watershed slope, and mixed forest land cover within the watershed. Effect sizes, which show the

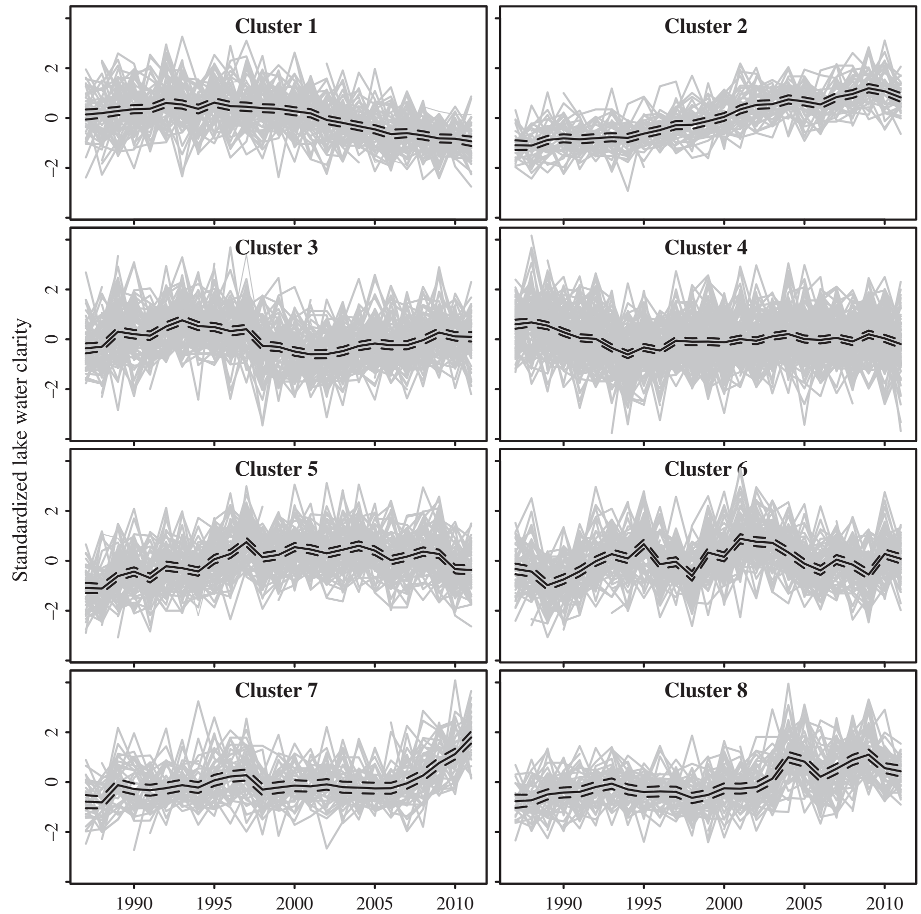

Fig. 3. Long-term (22+ yr) water clarity patterns for 601 lakes spread across an eight-state region. Standardized water clarity patterns (gray lines), common trend (solid black lines), and 95% credible intervals (dashed black lines). Clusters were determined using a kernel k-means clustering with dynamic time warping distance as the similarity measure. Average (common) trend for each cluster was determined using Bayesian random walk model.

average magnitude of functional responses of specific predictor variables (Appendix S1: Fig. S3), ranged from 0.12 to 0.57 (scale 0–1). Maximum lake depth was both the most important predictor in the RF model and the parameter with the largest effect size. Watershed slope (effect size = 0.43) and the amount of mixed forest within the watershed (effect size = 0.32) were intermediate in terms of variable importance but had large effect sizes. The percentage of woody wetland land cover within 500 m of a lake displayed the greatest disconnect between variable importance (third) and effect size (smallest), suggesting that while this was an important factor for predicting median water clarity, its effect on water clarity values was small.

On the other hand, while we could explain a large percentage of the variation in median water clarity among lakes, the RF model used to determine whether driver variables were related to each lake's cluster assignment (i.e., lakes with synchronous patterns) was not significant ($P > 0.05$). The overall accuracy of the classifier model was 26% (95% confidence interval 22–29%), and the kappa value was 15%, which is indicative of a poorly performing model (Fleiss 1981). Therefore, we did not attempt to determine which driver variables were related to long-term patterns and the effect sizes of those parameters. We also attempted to relate the long-term water clarity patterns in the 601 lakes to annual precipitation and mean annual temperature using temporally

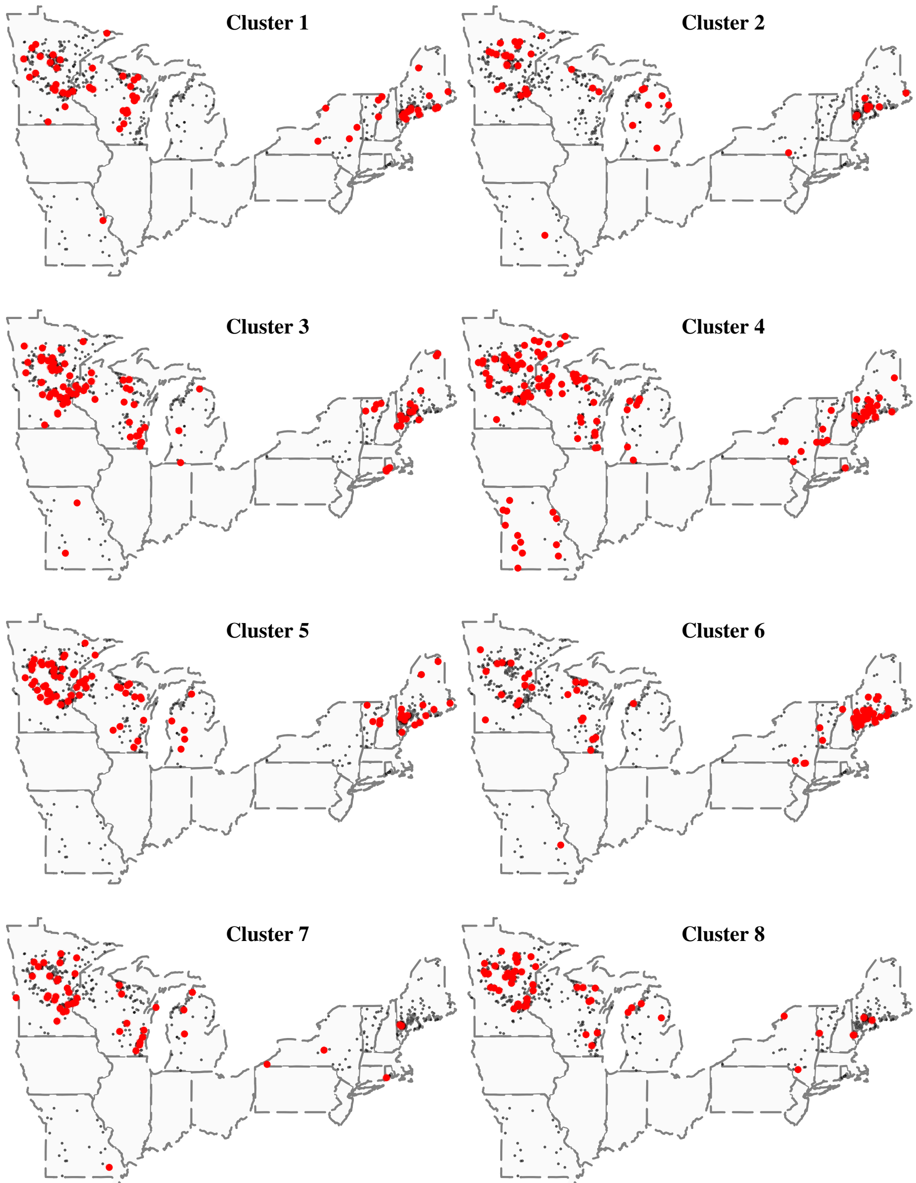

Fig. 4. Spatial location of lakes representing the eight distinct long-term water clarity patterns identified from the clustering analysis. Cluster-specific lakes are shown in red, and all lakes with long-term data in black.

explicit ARMAX models to determine whether we could simply model observed changes in water clarity from precipitation and temperature alone. These models also failed to explain a significant amount of the interannual variability in water clarity of individual lakes (Appendix S1: Fig. S4). The variance explained by ARMAX models ranged from 0% to 82% (median = 7.7%) with 75% of the models having $r^2 \leq 0.16$. Consequently, in addition to the ecological context of lakes having little influence on long-term water clarity patterns, our results suggest that simple climate measures such as annual precipitation and mean annual temperature are not related to interannual patterns of water clarity.

Discussion

Analysis of 25-yr records from 601 lakes revealed eight synchronous patterns of water

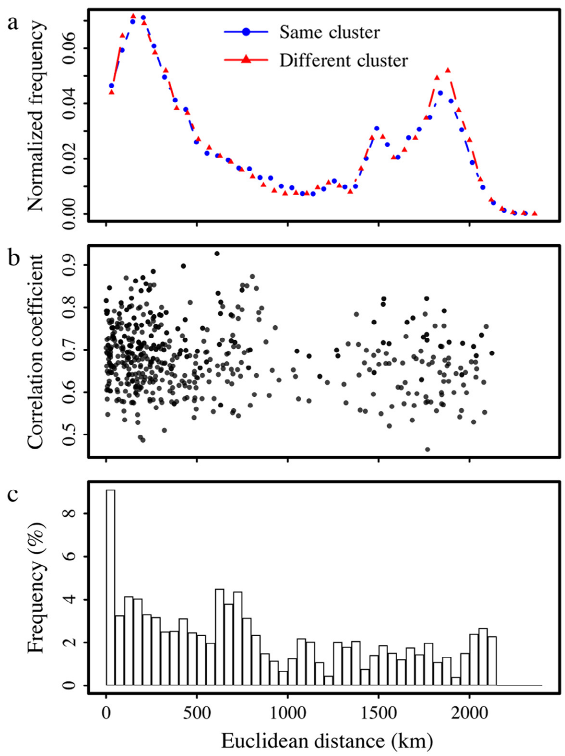

Fig. 5. Comparison of how similar water clarity values are between all pairs of lakes as a function of distance between lake pairs. (a) Normalized frequency of lakes that have similar trend vs. a different trend based on distance between lakes; (b) maximum synchrony in water clarity observed between one of the 601 lakes and the remaining 600 lakes as a function of how far the most synchronous lake is away, and (c) histogram showing the distribution of how far away the most synchronous lake is for each of the 601 lakes within the study region and weighted by the frequency of all lakes within each bin.

clarity change. Use of data-intensive analytical techniques allowed us to identify groups of synchronous time series that were robust to common problems in time series analyses including invalid assumptions about shapes of patterns and missing data. However, despite the occurrence of a relatively small number of temporal patterns, synchrony in water clarity among lakes was not spatially structured. Further, while the spatial variation in water clarity was well explained by 12 measures of ecological context, the determinants of spatial variation (or any other variable considered) in water clarity could not explain why groups of lakes had similar long-term patterns, providing evidence that the underlying assumption in space-for-time substitution studies —that drivers of ecosystem properties across space are similar to those through time—does not hold for lake water clarity and potentially other water quality variables.

Consistent with recent analyses of long-term observations in water clarity (Lottig et al. 2014), nutrients (Oliver et al. 2017), and temperature (O'Reilly et al. 2015), a majority of long-term patterns could not be significantly characterized by linear models and all but one of the synchronous patterns in this study were non-linear. Such pervasive non-linear patterns emphasize the basic challenge of identifying, understanding, and predicting temporal dynamics of ecosystems. However, given that ecosystem properties often demonstrate complex, non-linear temporal dynamics (Groffman et al. 2006), it is not surprising that most of the eight patterns were non-linear, nor that the patterns of change occurred at different temporal frequencies.

We did not find evidence for spatially structured synchrony in water clarity at any spatial scale. When lake dynamics are strongly correlated with a given driver, suites of lakes are expected to change in a similar manner at the same scale as the driver (Magnuson et al. 1990, Vogt et al. 2011). In particular, synchrony has frequently been linked to a variation in climate conditions for a range of ecosystem types and attributes (e.g., Batchelder et al. 2012, Defriez and Reuman 2017), including lakes (Baines et al. 2000). While water clarity can significantly differ between high and low precipitation years at a regional scale (Rose et al. 2017), we found that annual precipitation and mean annual temperature were not related to interannual variability in lake-specific water clarity. However, it is important to note that two to four decades of continuous data may be required to detect climate signals in water quality data (Henson et al. 2016) and statistical estimates from short time series can be uncertain (Ives et al. 2010). Thus, there is clearly a need to continue collecting data and expanding water quality time series to better understand how climatic trends may be influencing the patterns emerging in aquatic ecosystems at macroscales.

The absence of areas of synchrony argues against one or a few common drivers responsible for shaping temporal dynamics of water clarity (prediction 1) as it is clear from our results and others (e.g., O'Reilly et al. 2015) that lakes located in close spatial proximity are just as likely to have similar long-term patterns as they are to exhibit differences in those same long-term patterns. O'Reilly et al. (2015) concluded that "spatially structured synchrony in lakes is the exception not the norm" based on an analysis of global long-term lake temperature trends and our results reinforce this finding for water clarity as well with 2.5 times more lakes.

Finally, our results highlight that predictors related to spatial variation in ecosystem state can and do differ from those related to temporal variation. We were able to account for ~70% of the variation in average water clarity in 601 lakes. Across sub-continental to continental spatial scales, a similar proportion of variation in lake chemistry was explained by a combination of local and regional drivers (e.g., Read et al. 2015). However, the same set of drivers that explained spatial variation among the 601 lakes in this study did not explain differences among the temporal patterns in water clarity in these lakes, which potentially calls into question the utility of space-for-time substitutions for understanding temporal dynamics of water quality variables in lakes at large spatial scales.

Our inability to explain 25-yr temporal patterns in water clarity with well-known ecological context variables could be due to one of two reasons, both of which warrant further investigation. First, temporal patterns may be related to some ecological context feature that we did not include in the analysis. While we considered many of the variables known to be related to water clarity, data related to biotic drivers could not be included despite the fact that they have the potential to affect water clarity (e.g., Sanderson 1998, Baines et al. 2000, Walsh et al. 2016). Second, complex interactions among multi-scaled drivers likely contributed to our inability to explain temporal patterns. There is a growing number of examples of drivers at multiple spatial scales that interact to influence spatial patterns in ecosystem variables (Soranno et al. 2014), but quantifying these interactions is challenging and clearly an area for future research. At macroscales, one of the major challenges associated with identifying and quantifying these cross-scale interactions is that most of the data available to explain long-term water quality trends (along with many other ecosystems features) are static, but identifying spatio-temporal cross-scale interactions requires temporally dynamic variables quantified at broad spatial scales. Land use/cover variables based on remotely sensed images provide a particularly good example of this challenge; input data extracted from one or a few points in time often do not capture the temporal changes in landscape structure that may be influencing lake conditions.

In conclusion, this analysis of long-term patterns of water clarity and possible drivers contributes to understanding of spatial and temporal patterns of ecosystems at macroscales, including insight into broad-scale spatial patterns in the geography of synchrony and complex relationships between spatial and temporal patterns across ecosystems. These analyses also highlight the importance of long-term data and the need to continue generating long-term continuous water quality observations in order to better understand the long-term trends emerging in aquatic ecosystems at macroscales and how ecosystems are responding to the complex environmental changes that characterize our entry into the Anthropocene.

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Literature Cited

Arguez, A., I. Durre, S. Applequist, R. S. Vose, M. F. Squires, X. Yin, R. R. Heim Jr., and T. W. Owen. 2012. NOAA's 1981-2010 U.S. Climate normals: an overview. Bulletin of the American Meteorological Society 93:1687–1697.

Baines, S. B., K. E. Webster, T. K. Kratz, S. R. Carpenter, and J. J. Magnuson. 2000. Synchronous behavior of temperature, calcium, and chlorophyll in lakes of northern Wisconsin. Ecology 81:815–825.

Batchelder, H. P., D. L. Mackas, and T. D. O'Brien. 2012. Spatial-temporal scales of synchrony in marine zooplankton biomass and abundance patterns: a world-wild comparison. Progress in Oceanography 97:15–30.

Berndt, D. J., and J. Clifford. 1994. Using dynamic time warping to find patterns in time series. Proceedings of the AAAI Workshop on Knowledge Discovery in Databases 10:359–370.

Bruhn, L. C., and P. A. Soranno. 2005. Long Term (1974–2001) Volunteer monitoring of water clarity trends in Michigan lakes and their relation to ecoregion and land use/cover. Lake and Reservoir Management 21:10–23.

Defriez, E. J., and D. C. Reuman. 2017. A global geography of synchrony for terrestrial vegetation. Global Ecology and Biogeography 26:878–888.

Dugan, H. A., et al. 2017. Salting our freshwater lakes. Proceedings of the National Academy of Sciences of the United States of America 114:4453–4458.

Finazzi, F., R. Haggarty, C. Miller, M. Scott, and A. Fassò. 2015. A comparison of clustering approaches for the study of the temporal coherence of multiple time series. Stochastic Environmental Research and Risk Assessment 29:463–475.

Fleiss, J. L. 1981. Statistical methods for rates and proportions. Second edition. John Wiley and Sons, Hoboken, New Jersey, USA.

Fukami, T., and D. A. Wardle. 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. Proceedings of the Royal Society of London B: Biological Sciences 272:2105–2115.

Gebert, W. A., D. J. Graczyk, and W. R. Krug. 1987. Average annual runoff in the United States, 1951-80 (No. 710). US Geological Survey, Washington, D.C., USA.

Genuer, R., J. M. Poggi, and C. Tuleau-Malot. 2015. VSURF: an R package for variable selection using random forests. R Journal 7:19–33.

Groffman, P. M., et al. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13.

Gunn, J. M., E. Snucins, N. D. Yan, and M. T. Arts. 2001. Use of water clarity to monitor the effects of climate change and other stressors on oligotrophic lakes. Environmental Monitoring Assessment 67: 69–88.

Henson, S. A., C. Beaulieu, and R. Lampitt. 2016. Observing climate change trends in ocean biogeochemistry: when and where. Global Change Biology. https://doi.org/10.1111/gcb.13152

Hyndman, R. J., and Y. Khandakar. 2008. Automatic time series forecasting: the forecast package for R. Journal of Statistical Software 26:1–22.

Ives, A. R., K. C. Abbott, and N. L. Ziebarth. 2010. Analysis of ecological time series with ARMA(p, q) models. Ecology 91:858–871.

Jain, A. K., and R. C. Dubes. 1988. Algorithms for clustering data. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Jane, S. F., L. A. Winslow, C. K. Remucal, and K. C. Rose. 2017. Long-term trends and synchrony in dissolved organic matter characteristics in Wisconsin, USA, lakes: Quality, not quantity, is highly sensitive to climate. Journal of Geophysical Research Biogeosciences 122:546–561.

Jenny, J.-P., P. Francus, A. Normandeau, F. Lapointe, M.-E. Perga, A. Ojala, A. Schimmelmann, B. Zolitschka. 2016. Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused by rising local human pressure. Global Change Biology 22:1481–1489.

Lester, R. E., P. G. Close, J. L. Barton, A. J. Pope, and S. C. Brown. 2014. Predicting the likely response of data-poor ecosystems to climate change using space-for-time substitution across domains. Global Change Biology 20:3471–3481.

Liaw, A., and M. Wiener. 2002. Classification and regression by random forest. R News 2:18–22.

Lottig, N. R., P. Tan, T. Wagner, K. Cheruvelil, P. Soranno, E. Stanley, C. Scott, C. Stow, and S. Yuan. 2017. LAGOS-NE v.1.054.1 Lake water clarity time series (1987-2011), climate, and geophysical data for 601 lakes across a 17-state region of the United States. Environmental Data Initiative. https://doi.org/10.6073/pasta/d356b860d14635df1b604bbfb7e2a1d2

Lottig, N. R., et al. 2014. Long-term citizen collected data reveal geographical patterns and temporal trends in lake water clarity. PLoS ONE 9:e95769.

Magnuson, J. J., B. J. Benson, and T. K. Kratz. 1990. Temporal coherence in the limnology of a suite of lakes in Wisconsin, U.S.A. Freshwater Biology 23:14–159.

Magnuson, J. J., B. J. Benson, and T. K. Kratz. 2004. Patterns of coherent dynamics within and between lake districts at local to intercontinental scales. Boreal Environment Research 9:359–369.

Magnuson, J. J., et al. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science 289:1743–1746.

Oliver, S. K., S. M. Collins, P. A. Soranno, T. Wagner, E. H. Stanley, JR Jones, CA Stow, NR Lottig. 2017. Unexpected stasis in a changing world: lake nutrient and chlorophyll trends since 1990. Global Change Biology. https://doi.org/10.1111/gcb13810

O'Reilly, C. M., et al. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters 42:10, 773–10781.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. Ecosystems 10:790–796.

Pickett, S. T. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 In G. E. Likens, editor. Long-term studies in ecology. Springer, New York, New York, USA.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Read, E. K., L. Carr, L. De Cicco, H. A. Dugan, P. C. Hanson, J.A. Hart, J. Kreft, J.S. Read, and L.A. Winslow. 2017. Water quality data for national-scale aquatic research: the Water Quality Portal. Water Resources Research 53:1735–1745.

Read, E. K., et al. 2015. The importance of lake-specific characteristics for water quality across the continental United States. Ecological Applications 25:943–955.

Rose, K. C., S. R. Greb, M. Diebel, and M. G. Turner. 2017. Annual precipitation regulates spatial and temporal drivers of lake water clarity. Ecological Applications 27:623–643.

Rousseeuw, P. J. 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. Computational and Applied Mathematics 20: 53–65.

Sanderson, B. L. 1998. Factors regulating water clarity in northern Wisconsin lakes. Thesis. University of Wisconsin, Madison, Wisconsin, USA.

Schölkopf, B., A. Smola, and K.-R. Müller. 1998. Nonlinear component analysis as a kernel eigenvalue problem. Neural Computation 10:1299–1319.

Soranno, P. A., et al. 1999. Spatial variation among lakes within landscapes: ecological organization along Lake Chains. Ecosystems 2:395–410.

Soranno, P. A., et al. 2014. Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. Frontiers in Ecology and the Environment 12:65–73.

Soranno, P. A., et al. 2015. Building a multi-scaled geospatial temporal ecology database from disparate data sources: fostering open science and data reuse. GigaScience 4:28.

Soranno, P. A., et al. 2017. LAGOS-NE: a multi-scaled geospatial temporal database of lake ecological context and water quality for thousands of U.S. Lakes. GigaScience. https://doi.org/10.1093/gigascience/gix101

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practices: pattern and process. Springer-Verlag, New York, USA.

Vogt, R. J., J. A. Rusak, A. Patoine, and P. R. Leavitt. 2011. Differential effects of energy and mass influx on the landscape synchrony of lake ecosystems. Ecology 92:1104–1114.

Wagner, T., S. R. Midway, T. Vidal, B. J. Irwin, and J. R. Jackson. 2016. Detecting unusual temporal patterns in fisheries time series data. Transactions of the American Fisheries Society 145:786–794.

Walsh, J. R., S. R. Carpenter, and M. J. Vander Zanden. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences of the United States of America 113:4081–4085.

Walter, J. A., L. W. Shepard, T. L. Anderson, J. H. Kastens, O. N. Bjornstad, A. M. Liebhold, D. C. Reuman. 2017. The geography of spatial synchrony. Ecology Letters. https://doi.org/10.1111/ele.12782

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

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